A Mathematical Model for Invasion Range of Population Dispersing Through Patchy Environment

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Abstract

In this work, to focus the question of how the dispersion of an invading population is affected by the spatial distribution of patches that have resource available for its settlement and reproduction, we develop a mathematical model with a simple stochastic process, and analyze it. We classify those patches into three classes: *free*, *occupied* and *abandoned*, depending on the state of patch use by the population. We especially consider the range expanded by invaded patches, the *invaded range* R, assuming a certain generalized relation between R and the total number of invaded patches k, making use of an index, a sort of *fractal dimension*, to characterize the spatial distribution of invaded patches. We show that the expected velocity is significantly affected by the nature of spatial distribution of resource patches, and is temporally variable. When the invading population finally goes extinct at a moment, the terminal size of invaded range at the moment is closely related to the nature of spatial distribution of resource patches, which is explicitly demonstrated by our analysis.

keywords: invasion – metapopulation – patch – fractal dimension – velocity – stochastic process

INTRODUCTION

In nature, a variety of species expand their spatial distribution depending on their ecological characteristics, settling their habitats composed of patchy envi-

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ronments, for instance, of trees, of wetland, or of mountains (Anderson and May 1986; Andow *et al.* 1990; Dwyer *et al.* 1997; Jeger 1989; Johnson *et al.* 1992; Levin 1992; Neuhauser 2001; O'Neill *et al.* 1988; Pascual *et al.* 2002; Russell *et al.* 1992; Turner *et al.* 2001; van den Bosch *et al.* 1997; With 2002). In general, such patchy environment corresponds to the spatially patchy distribution of resources required for the settlement and the reproduction of population. In human case, we may consider the geographical place favorable to construct town or village as such patch. Since such spatial distribution of resources could be reflected to the resulted population distribution, the spatial distribution of population would appear patchy in not a few cases. Such patchiness of population distribution can be discussed from the viewpoint of fractal, too (Gautestad and Mysterud 1994; Haskell *et al.* 2002; Keymer *et al.* 2000; Mandelbrot 1982; Morse *et al.* 1985; Palmer 1988; Russell *et al.* 1992; Sugihara and May 1990; Turner *et al.* 2001; With 1994; With and King 1999; With 2002).

In this paper, with a mathematical model, we consider the effect of spatial distribution of resource patches on the nature of spatial expansion of population distribution. Especially we focus on the velocity of its spatial expansion from the original place where the invasion of population begins. The velocity of spatial expansion of invaded region must be affected by the nature of spatial distribution of resource patches. Velocity of spatial expansion of population distribution has been theoretically discussed in various contexts mostly with mathematical models of reaction-diffusion system (Brauer and Castillo-Chávez 2001; Diekamann and Heesterbeek 2000; Fagan *et al.* 2002; Murray 2002a; Murray 2002b; Shigesada and Kawasaki 1997), integro-differential or integro-difference equations (Atkinson and Reuter 1976; Brown and Carr 1977; Kot and Schaffer 1986; Medlock and Kot 2003; Mollison 1977; Neubert *et al.* 2000), percolation theory or network theory (Bailey el al. 2000; Grassberger 1983; Keeling 1999; Meyers *et al.* 2003; Newman 2002; Otten *et al.* 2004; Sander *et al.* 2002; Stauffer and Aharony 1991; Tan *et al.* 2000) , cellular automaton or lattice dynamics (Brown and Bolker 2004; Filipe and Gibson 1998; Filipe *et al.* 2004; Levin and Durrett 1997; Sato *et al.* 1994). Especially, mathematical models with percolation theory or network theory have been attracting researchers who are interested in the invasion threshold which is the critical condition to determine weather the infection stops in a finite period or keeps its spatial expansion.

In contrast, we here try to discuss the velocity with a mathematical model of stochastic process, analyzing the expected velocity. In our modeling, to incorporate the effect of heterogeneous spatial distribution of resource patches on the spatial expansion of invaded region, we characterize the spatial distribution of resource patches with an index, *fractal dimension* (Hastings and Sugihara 1993; Mandelbrot 1982), and introduce it into the model. So our model describes the population dynamics with a stochastic process, and the spatial expansion of invaded region with a fractal nature of spatial distribution of resource patches. This type of combination of population dynamics and spatial expansion may be regarded as an approximation for the real interrelationship between them. We show that our modeling would be useful to get theoretical insights or develop the more advanced or practical model about the spatial expansion of invaded region.

MODELING

Assumptions

In our modeling, we classify the patches into three classes, depending on the state of patch use by the population: *free*, *occupied* and *abandoned*. Occupied patch means the patch where the population is consuming the resource in it, making its reproduction. Abandoned patch does the patch exhausted its resource and abandoned by the population. Free patch is the patch that has not been invaded yet. Population dispersion occurs only from occupied patches, and the disperser invades some free patches. Such invasion to free patches causes the expansion of invaded region determined by the population distribution in space.

As for the class of abandoned patch, in another contexts, we may regard it as the population extinction within the patch. If the considered population is of a harmful insect to be exterminated, such abandoned patch may be regarded as the artificially exterminated patch aggregating the insect. In our modeling, it is essential that the patch belonging to the class of abandoned patch is not to provide the disperser from it or to attract any disperser into it. In this sense, the abandoned patch may be regarded as the *isolated* patch.

With such abandonment of patches, our model could be regarded as for a spatial dispersion of population which appears as an outbreak at a certain habitat and moves away from the origin, consuming every available resource, for instance, like a grasshopper outbreak.

Our modeling assumes the followings:

- Invasion rate depends only on the total number of occupied patches.
- Only free patch could be invaded.
- Abandoned patch is never invaded or used again.
- Settlement and abandonment of a patch are independent of those of any other patches.

We should remark that the invasion rate is determined by the number of patches instead of population size like (Seno and Matsumoto 1996). Population size of disperser would be closely related to the population size in occupied patches as the source of dispersers. Hence, in our modeling of this paper, we assume that the population size of disperser would be positively related to the number of occupied patches.

We do not consider the population dynamics within each patch, but classify the patch as mentioned above in terms of its use by the population. In this sense, our modeling can be regarded as a sort of metapopulation dynamics (for instance, see Hanski 1994a; Hanski 1994b; Hanski 1999; Johnson *et al.* 1992; Keymer *et al.* 2000; Ovaskainen and Hanski 2001; With and King 1999), Besides, according to the classification of patches into three classes and their definitions, our modeling may be regarded as corresponding to a kind of SIR epidemic dynamics (for instance, see Brauer and Castillo-Chávez 2001; Diekamann and Heesterbeek 2000; Murray 2002a; Shigesada and Kawasaki 1997).

In this paper, we focus the number of *occupied* patches, h, and that of *invaded* patches which consist of occupied and abandoned, k. Invaded patch

is an occupied or abandoned one, that is, a patch which has experienced the invasion. The number of abandoned patches is given by the difference $k - h$.

Model Construction

Probability distribution for the state of patch use

We donote by $P(k, h, t)$ the probability of state such that there are k *invaded* patches and h *occupied* patches at time t in the considered system. To determine the probability $P(k, h, t)$, we consider the possible transitions of state in sufficiently small time interval $(t, t + \Delta t]$ with our modeling assumptions, and derive the following system of differential equations that govern the temporal variation of probability $P(k, h, t)$:

$$\frac{dP(k,h,t)}{dt} = -(\beta+\gamma)hP(k,h,t)+\gamma(h+1)P(k,h+1,t)+\beta(h-1)P(k-1,h-1,t), \tag{1}$$

for $k \geq 2,\ h \geq 1,\ k \geq h+1$, and the following additional two:

$$\frac{dP(k,0,t)}{dt} = \gamma P(k,1,t), \tag{2}$$

$$\frac{dP(k,k,t)}{dt} = -k(\beta+\gamma)P(k,k,t) + (k-1)\beta P(k-1,k-1,t) \tag{3}$$

for $k \geq 1$. Parameter β is the settlement rate, and γ the abandonment rate. If the considered population is of a harmful insect to be exterminated, γ may be regarded as the extermination rate for a patch aggregating the insect.

The essence of modeling for the derivation of above equations is as follows: Probability that a free patch is invaded during sufficiently small period Δt by the disperser from an occupied patch is assumed to be given by $\beta\Delta t + o(\Delta t)$ independently of the distance between these patches. Since we assume that the settlement to a free patch by the disperser from an occupied patch is independent of that by any other occupied one, the probability that a free patch is invaded by any of dispersers from h occupied ones becomes $\beta h\Delta t + o(\Delta t)$. Probability that an occupied patch is abandoned is assumed to be given by $\gamma\Delta t + o(\Delta t)$. When there are h occupied patches, the probability that only one of them is abandoned is given by the probability for the abandonment of an occupied patch and that for the non-abandonment of the other $h-1$ occupied ones. Therefore, the probability that only one occupied patch is abandoned during sufficiently small period Δt is given by $\gamma h\Delta t + o(\Delta t)$. Probability that more than one occupied patches are abandoned is to be $o(\Delta t)$. Moreover, from the assumption of independence between settlement and abandonment, the probability that both settlement and abandonment occur during the time period Δt is given by $o(\Delta t)$, because the probability for each of them has the order Δt.

Initial condition

We assume that the invasion begins with a patch at time 0, so that the initial condition is given by

$$P(k,h,0) = \begin{cases} 1 & \text{if } k = h = 1, \\ 0 & \text{otherwise.} \end{cases} \tag{4}$$

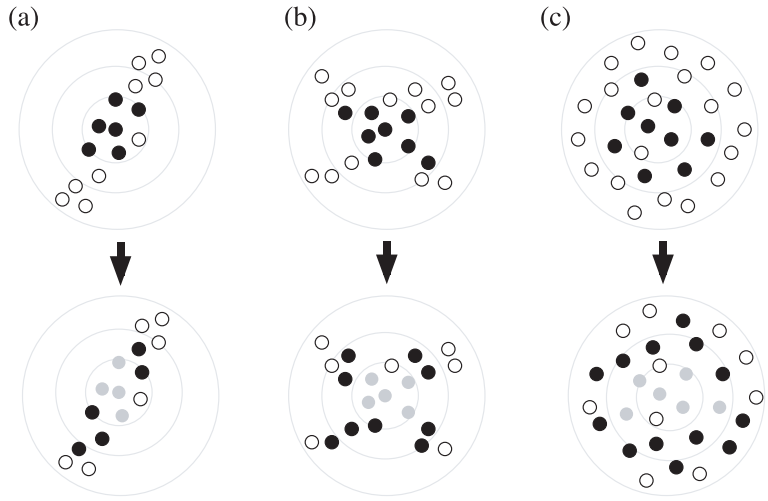

Figure 1: Illustrative explanation of the relation of the fractal dimension d to the spatial pattern of patch distribution. Schematic process of settlement and abandonment is also shown. White disc indicates free patch, black occupied, and grey abandoned. (a) $d \approx 1$; (b) $1 < d < 2$; (c) $d \approx 2$.

An invader species is assumed to be introduced into the considered environment in artificial or natural reason. Then the invader species settles in a patch which is the original place of invasion.

Expansion of invaded range

Next, we consider the range expanded by invaded patches, say, the *invaded range*. We characterize the invaded range by the minimal diameter R which includes all invaded patches.

In the case when the invaded range expands in every direction with the same probability, the shape of invaded region can be approximated by the disc, and therefore, when the spheric nature of the earth can be negligible and be approximated well by the plane, the range R approximately has the following relation with the number of invaded patches k: $k \propto R^2$. However, since the expansion of invaded range is constrained by the spatial distribution of resources, which could be in general heterogeneous, the shape is possibly inhomogeneous in direction. It is likely that the shape can be characterized by its *fractal* nature (for the concept of "fractal", for instance, see Hastings and Sugihara 1993; Mandelbrot 1982; Sugihara and May 1990). To deal with such case, we assume the generalized relation between the invaded range and the total number of invaded patches as follows:

$$k \propto R^d \qquad (1 \leq d \leq 2), \tag{5}$$

where the power d characterizes the spatial pattern of invaded region occupied by invaded patches (Fig. 1). Power d is called *cluster dimension* or *mass dimension*, which is a sort of *fractal dimension* (Hastings and Sugihara 1993; Mandelbrot 1982). When $d \approx 2$, the spatial distribution of invaded patches

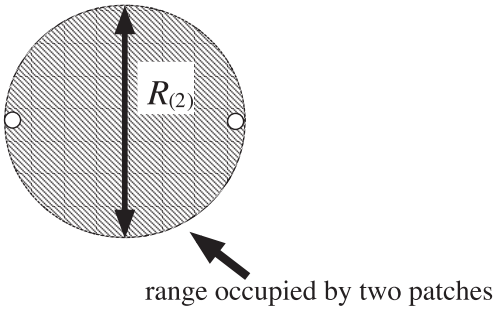

Figure 2: Illustrative explanation of range $R_{(2)}$.

can be approximated well by a disc. When $d \approx 1$, the distribution can be approximately regarded as one dimensional, that is, the invaded patches can be regarded to be arrayed along a curve.

This idea of introduction of fractal nature into the mathematical model for the spatial patch distribution is the same as that in Seno (1993). This modeling may be regarded as a sort of mean-field approximation for the percolation process on an anisotropic/fractal lattice or the growing network (Bailey el al. 2000; Grassberger 1983; Meyers *et al.* 2003; Newman 2002; Otten *et al.* 2004; Sander *et al.* 2002; Stauffer and Aharony 1991; Tan *et al.* 2000). In such previous models, the main problem was the invasion threshold which is the critical condition to determine if the invasion stops in a finite period or keeps its spatial expansion. In contrast, we are now going to focus the velocity of spatial expansion of invaded range.

For convenience to apply the relation (5) for our modeling, we now define the proportional constant C:

$$k = CR^d \qquad (1 \leq d \leq 2). \tag{6}$$

Next, conventionally we define the mean distance $\overline{R}_{(2)}$ from one patch to the nearest neighbour (Fig. 2). In our modeling, $\overline{R}_{(2)}$ is assumed to be corresponding to the expected invaded range expanded by two invaded patches, that is, $k = 2$. Therefore, from (6), we assume that

$$2 = C\overline{R}^d_{(2)}. \tag{7}$$

Hence, from (6) and (7), for the *expected* number of invaded patches $\langle k \rangle_t$ at time t, we assume the following relation for the *expected* invaded range $\overline{r}_t$ at time t:

$$\langle k \rangle_t = 2\overline{r}^d_t \qquad (1 \leq d \leq 2), \tag{8}$$

where $\overline{r}_t$ is the expected invaded range measured in the mean distance $\overline{R}_{(2)}$: $\overline{r}_t \equiv \overline{R}_t / \overline{R}_{(2)}$.

Further, we can define the *expected* velocity $\overline{V}_t$ of expansion of the invaded range at time t by

$$\overline{V}_t = \frac{d\overline{r}_t}{dt}.$$

So, from (8), we can obtain the following relation between the expected velocity $\overline{V}_t$ and the expected number $\langle k \rangle_t$ of invaded patches at time t:

$$\overline{V}_t = \frac{1}{d}\left(\frac{1}{2}\right)^{1/d} \langle k \rangle_t^{1/d-1} \cdot \frac{d\langle k \rangle_t}{dt}. \tag{9}$$

ANALYSIS

Expected Number of Occupied Patches

We denote by $\langle h \rangle_t$ the *expected* number of occupied patches at time t. It is defined by

$$\langle h \rangle_t = \sum_{k=1}^{\infty} \sum_{h=1}^{k} hP(k,h,t). \tag{10}$$

From (1) and (3), we can obtain the following:

$$\frac{d}{dt}\langle h \rangle_t \quad = \quad (\beta - \gamma)\langle h \rangle_t,$$

and then

$$\langle h \rangle_t \quad = \quad e^{(\beta-\gamma)t}, \tag{11}$$

where we used the initial condition (4) for (10): $\langle h \rangle_0 = 1$.

Expeceted Number of Invaded Patches

As for invaded patches, we denote by $\langle k \rangle_t$ the *expected* number of invaded patches at time t, defined by

$$\langle k \rangle_t = \sum_{k=1}^{\infty} k \left\{ \sum_{h=0}^{k} P(k,h,t) \right\}. \tag{12}$$

From (1), (2) and (3), we can obtain the following:

$$\frac{d}{dt}\langle k \rangle_t \quad = \quad \beta \langle h \rangle_t.$$

With (11), we can solve this differential equation and get

$$\langle k \rangle_t \quad = \quad \frac{\beta}{\beta - \gamma}\{e^{(\beta-\gamma)t} - 1\} + 1, \tag{13}$$

where we used the initial condition (4) for (12): $\langle k \rangle_0 = 1$.

Now, we consider the saturated value of $\langle k \rangle_t$ as $t \to \infty$. From (13), for $\beta \geq \gamma$ when the settlement rate is not less than the abandonment rate, $\langle k \rangle_t$ becomes positively infinite as $t \to \infty$. On the other hand, for $\beta < \gamma$ when the abandonment rate is greater than the settlement rate, the saturated value is as follows:

$$\langle k \rangle_{t \to \infty} = \frac{\gamma}{\gamma - \beta}. \tag{14}$$

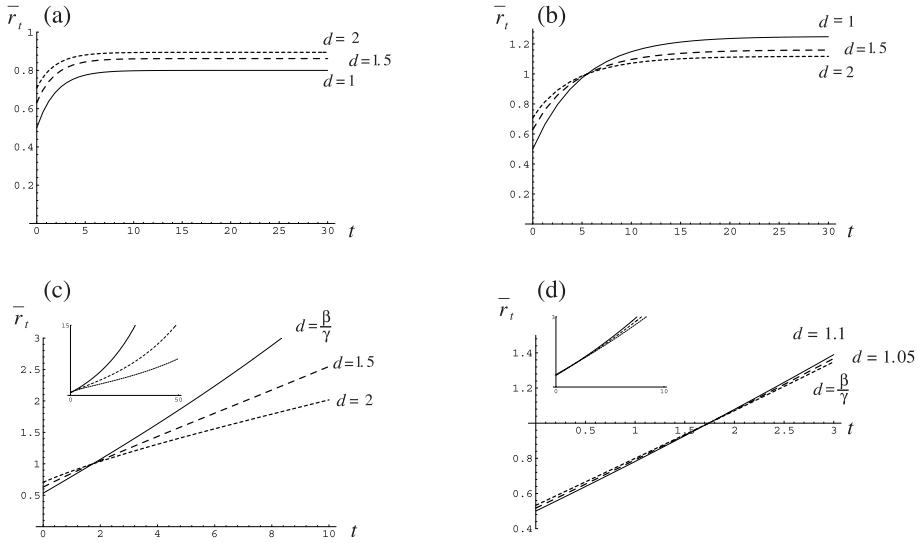

Figure 3: Temporal development of the expected invaded range. (a) $0 < \beta/\gamma < 1/2$, numerically drawn for $\beta = 0.3$ and $\gamma = 0.8$; (b) $1/2 \leq \beta/\gamma \leq 1$, for $\beta = 0.3$ and $\gamma = 0.5$; (c) $1 < \beta/\gamma < d$, for $\beta = 0.55$ and $\gamma = 0.5$; (d) $\beta/\gamma \geq d$, for $\beta = 0.55$ and $\gamma = 0.5$.

Expected Invaded Range

Since, from (8),

$$\overline{r}_t = \left(\frac{\langle k \rangle_t}{2} \right)^{1/d}, \tag{15}$$

we can consider how the expected invaded range $\overline{r}_t$ depends on the fractal dimension d of the spatial distribution of patches, making use of (13). For $0 < \beta/\gamma < 1/2$, when the abandonment rate is sufficiently greater than the settlement rate, the expected invaded range $\overline{r}_t$ gets larger as d is larger (Fig. 3(a)). This means that the invaded range is expected to become wider as patches are more uniformly distributed. In contrast, for $\beta/\gamma \geq 1/2$, the expected invaded range gets smaller as d is larger (Fig. 3(b-d)). In this case, the invaded range is expected to be narrower as the patches are more uniformly distributed. Therefore, in our model, only if the settlement rate is smaller than half of the abandonment rate, the more uniform distribution of free patches causes the wider expected invaded range (Fig. 4).

Now, we consider the saturated value of expected invaded range as $t \to \infty$. From (13) and (15), for $\beta \geq \gamma$, $\overline{r}_t$ becomes positively infinite as $t \to \infty$ (Fig. 3(c, d)). For $\beta < \gamma$, it saturates to the following value as $t \to \infty$ (Fig. 3(a, b)):

$$\overline{r}_{t\to\infty} = \left(\frac{\langle k \rangle_{t\to\infty}}{2} \right)^{1/d} = \left(\frac{1}{2} \cdot \frac{\gamma}{\gamma - \beta} \right)^{1/d}. \tag{16}$$

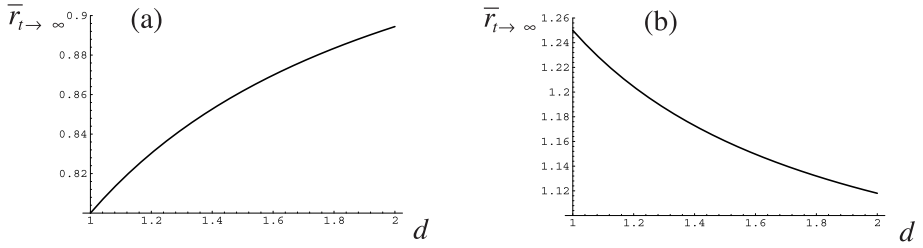

Figure 4: d-dependence of the saturated value of expected invaded range. (a) $0 < \beta/\gamma < 1/2$, numerically drawn for $\beta = 0.3$ and $\gamma = 0.8$; (b) $\beta/\gamma \geq 1/2$, for $\beta = 0.3$ and $\gamma = 0.5$.

Expected Expansion Velocity of Invaded Range

From (13), we can get the following expected expansion velocity of invaded range, $\overline{V}_t$ defined by (9):

$$\begin{aligned} \overline{V}_t &= \frac{1}{d}\left(\frac{1}{2}\right)^{1/d} \beta e^{(\beta-\gamma)t}\left[\frac{\beta}{\beta-\gamma}\{e^{(\beta-\gamma)t}-1\}+1\right]^{1/d-1} \\ &= \frac{1}{d}\left(\frac{1}{2}\right)^{1/d} \langle k\rangle_t^{1/d-1}\left\{(\beta-\gamma)\left(\langle k\rangle_t - 1\right)+\beta\right\}. \end{aligned} \tag{17}$$

When $\beta/\gamma \leq 1$, that is, when the abandonment rate is not less than the settlement rate, the expected velocity $\overline{V}_t$ monotonically decreases in time (Fig. 5(a)).

When $1 < \beta/\gamma < d$, that is, when the settlement rate is greater than the abandonment rate and small enough so as β/γ less than d, the expected velocity $\overline{V}_t$ decreases in the earlier period and then turns to increase monotonically (Fig. 5(b)). We denote by t_c the time at the moment when the expected velocity turns from decreasing to increasing. From (9), we can get

$$t_c = \frac{1}{\beta-\gamma}\ln\frac{\gamma}{\beta}d. \tag{18}$$

When $\beta/\gamma \geq d$, that is, when the settlement rate is sufficiently greater than the abandonment rate, the expected velocity $\overline{V}_t$ monotonically increases in time (Fig. 5(c)).

In case of $\beta/\gamma > 1$, from (17) for sufficiently large t,

$$\overline{V}_t \approx \frac{1}{d}\left(\frac{1}{2}\right)^{1/d}\beta\left[\frac{\beta}{\beta-\gamma}\right]^{1/d-1} e^{\{(\beta-\gamma)/d\}t} = \frac{1}{d}\left(\frac{1}{2}\right)^{1/d}(\beta-\gamma)\langle k\rangle_t^{1/d}. \tag{19}$$

Therefore, if $\beta/\gamma > 1$, the expected velocity $\overline{V}_t$ exponentially increases for sufficiently large t, with the exponent inversely proportional to the fractal dimension d.

Consequently we can see how the expected velocity $\overline{V}_t$ depends on the fractal dimension d of the spatial distribution of patches. The expected velocity gets smaller as d is larger (Fig. 5(a-c)) for any value of β/γ. Therefore, in our model, the more uniform distribution of patches causes the slower expansion of invaded range.

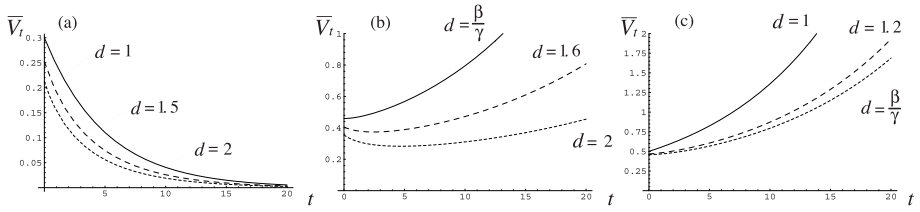

Figure 5: Temporal variation of the expected expansion velocity of invaded range. (a) $0 < \beta/\gamma \leq 1$, numerically drawn for $\beta = 0.3$ and $\gamma = 0.5$; (b) $1 < \beta/\gamma < d$, for $\beta = 0.5$ and $\gamma = 0.4$; (c) $\beta/\gamma \geq d$, for $\beta = 0.5$ and $\gamma = 0.4$.

Probability for Termination of Invasion

We denote by $P_{h=0}$ the probability for the termination of invasion. Once all the occupied patches disappear in space because of abandonment, the invasion can no longer continue and restart. This means the termination of invasion. If the invasion terminates at time t, the state of patch use at time $t-\Delta t$ should be with only one occupied patch for sufficiently small Δt, and it should be adandoned during Δt without causing any new settlement. When the number of invaded patches is k at time t, the probability for this event is given by

$$P(k,1,t)[1-\beta\Delta t - o(\Delta t)]\cdot[\gamma\Delta t + o(\Delta t)] = \gamma P(k,1,t)\Delta t + o(\Delta t). \qquad (20)$$

Therefore, the probability for the termination of invasion between $t-\Delta t$ and t is given by the sum of (20) over any possible k.

Making use of the probability generating function (p.g.f.) defined by

$$f(x,y,t) = \sum_{k=1}^{\infty}\sum_{h=0}^{k} P(k,h,t)x^k y^h, \qquad (21)$$

we can derive the probability $P_{h=0}$ for the termination of infection (as for the detail of p.g.f., see Appendix):

$$\begin{aligned} P_{h=0} &= \int_0^\infty \gamma \sum_{k=1}^{\infty} P(k,1,t)dt \\ &= \int_0^\infty \gamma \cdot \left.\frac{\partial f}{\partial y}\right|_{x=1,y=0} dt \\ &= \int_0^\infty \gamma \cdot \frac{e^{-(\beta-\gamma)t}\{(\beta-\gamma)/\beta\}^2}{1-e^{-(\beta-\gamma)t}\gamma/\beta} dt \\ &= \min\left\{\frac{\gamma}{\beta}, 1\right\}. \end{aligned} \qquad (22)$$

When the probability $P_{h=0}$ is 1, that is the case when the abandonment rate is greater than the settlement rate, the invasion certainly terminates in a finite time (Fig. 6).

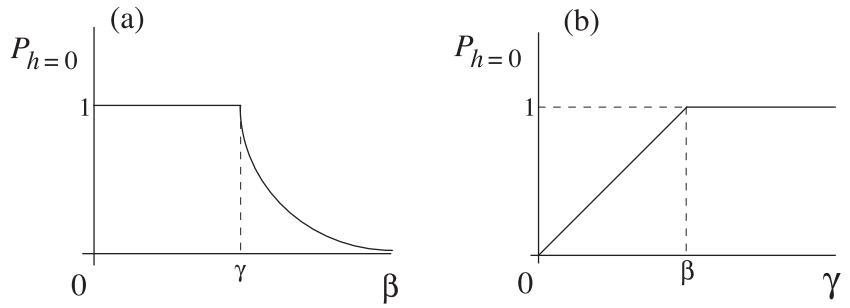

Figure 6: Parameter dependence of the probability for the termination of invasion, $P_{h=0}$. (a) β-dependence; (b) γ-dependence.

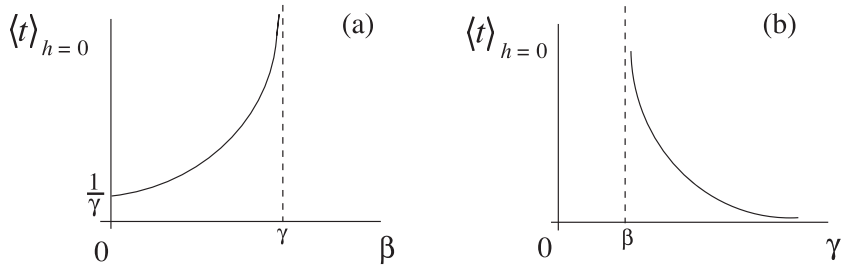

Figure 7: Parameter dependence of the expected time for the termination of invasion $\langle t \rangle_{h=0}$. (a) β-dependence; (b) γ-dependence.

Expected Time for Termination of Invasion

We denote by $\langle t \rangle_{h=0}$ the expected time at which the termination of invasion occurs. From the arguments in the previous section, we can obtain it as follows:

$$\begin{aligned} \langle t \rangle_{h=0} &= \int_0^\infty t\gamma \sum_{k=1}^{\infty} P(k,1,t)dt \\ &= \begin{cases} +\infty & \text{if } \beta \geq \gamma; \\ \dfrac{1}{\beta} \ln \dfrac{\gamma}{\gamma - \beta} & \text{if } \beta < \gamma. \end{cases} \end{aligned} \tag{23}$$

For $\beta < \gamma$ when the abandonment rate is greater than the settlement rate, we can expect the invasion terminates at a finite time $\langle t \rangle_{h=0}$ (Fig. 7).

Expected Number of Invaded Patches at Termination of Invasion

We denote by $\langle k \rangle_{h=0}$ the expected number of invaded patches at the termination of invasion. Integral $\int_0^\infty \gamma P(k,1,t)dt$ gives the probability that the number of invaded patches is k at the termination of invasion. Therefore, making use of

the p.g.f. (A.28), we can get the following:

$$\begin{aligned}
\langle k\rangle_{h=0} &= \sum_{k=1}^{\infty} k \int_0^{\infty} \gamma P(k,1,t)dt \\
&= \gamma \int_0^{\infty} \sum_{k=1}^{\infty} kP(k,1,t)dt \\
&= \gamma \int_0^{\infty} \frac{\partial}{\partial y}\left(\frac{\partial f}{\partial x}\right)\Big|_{x=1,y=0} dt \\
&= \frac{\gamma}{\gamma-\beta}. \qquad (24)
\end{aligned}$$

From (14) and (24), we see that the expected number of invaded patches at the termination of invasion, $\langle k\rangle_{h=0}$, is identical to the saturated value of $\langle k\rangle_t$, $\langle k\rangle_{t\to\infty}$:

$$\langle k\rangle_{h=0} = \langle k\rangle_{t\to\infty}.$$

Therefore, $\langle k\rangle_{h=0}$ has its natures same as for $\langle k\rangle_{t\to\infty}$. Hence, the expected range at the termination of invasion is also equal to the saturated range of $\overline{r}_t$, $\overline{r}_{t\to\infty}$.

DISCUSSION

In this work, to focus the question of how the dispersion of an invading population is affected by the spatial distribution of patches that have resource available for its settlement and reproduction, we developed a mathematical model with a simple stochastic process, and analyzed it.

In reality, a variety of species expand their spatial distribution depending on their ecological characteristics, settling their habitats composed of fragmentated/patchy environments, for instance, of trees, of wetland, or of mountains (Brown and Bolker 2004; Caraco *et al.* 2001; Drenth 2004; Johnson *et al.* 1992; Neuhauser 2001; O'Neill *et al.* 1988; Otten *et al.* 2004; Pascual *et al.* 2002; Russell *et al.* 1992; Turner *et al.* 2001; van den Bosch *et al.* 1997; With 2002). So we can regard each of such spatially fragmentated habitats as the patch available for an invader population. In human case, we may consider such patch as the geographical place favorable to construct town or village.

We assumed that those available patches are classified into three classes: *free*, *occupied* and *abandoned*, depending on the state of patch use by the population. Occupied patch is where the population is consuming the resource in it, making its reproduction. Abandoned patch is where the resource is exhausted and the population abandoned. It may be regarded as the patch where the population goes extinct within it. Free patch is the patch that has not been invaded yet. Dispersers/migrators appear only from occupied patches, and the dispersers/migrators invade into some free patches. Such invasion to free patches causes the expansion of considered population distribution in space.

In our modeling, we do not consider the population dynamics within each patch, but classify the patch as mentioned above in terms of its use by the population. In this sense, our modeling can be regarded as a sort of *metapopulation dynamics* (Hanski 1999; Johnson *et al.* 1992; Keymer *et al.* 2000; With and King

1999), or more specifically a sort of *stochastic patch occupancy modeling* (Hanski 1994a; Hanski 1994b; Ovaskainen and Hanski 2001). Besides, according to the classification of patches into three classes and their definitions, our modeling may be regarded as corresponding to a kind of SIR epidemic dynamics (for instance, see Brauer and Castillo-Chávez 2001; Diekamann and Heesterbeek 2000; Murray 2002a; Shigesada and Kawasaki 1997).

We considered the probability for the state such that k *invaded* and h *occupied* patches exist at time t. Invaded patches consist of occupied and abandoned ones, that is, those which have experienced the invasion. We constructed the system of differential equations to describe the temporal variation of the probability distribution, and analyzed it. Then, we developed the mathematical modeling for the range expanded by invaded patches in space, the *invaded range*, which can be characterized by the *expected* minimal diameter R which includes all invaded patches. We assumed a certain generalized relation between R and the total number of invaded patches k, making use of an index called *cluster dimension* or *mass dimension*, that is a sort of *fractal dimension* (Hastings and Sugihara 1993; Mandelbrot 1982; Sugihara and May 1990), to characterize the spatial distribution of patches. With the relation, we derived the temporal variations of expected invaded range and its expected expansion velocity. Although we applied the fractal dimension to incorporate some notion of space or heterogeneity in space into our model, the location or the configuration of patches in space is not explicitly introduced in it. In this sense, our model could be regarded as one between non-spatial population dynamics model and numerical spatial dynamic model, and may be a kind of *semi-spatial model* as called by (Filipe *et al.* 2004).

In our modeling, a free patch is invaded with probability proportional to the *total number* of occupied patches, that is, the total number of habitats with inhabiting population. Our modeling assumption may be translated as follows: the invasion for a free patch would be proportional to the total population size of all occupied patches, as in Seno and Matsumoto (1996) which analyzes a mathematical model for population dynamics to expand its spatial distribution with patch creation by the existing population. This is not exactly comparable to our model in this paper, because ours is of metapopulation dynamics with a given spatial distribution of resource patches, without considering the population dynamics within each patch or the patch size.

From the results of our analysis on the mathematical model, we found that the expected velocity is significantly affected by the nature of spatial distribution of resource patches, and is temporally variable, differently from those results frequently derived for the mathematical model with the reaction-diffusion system in continuous and homogeneous space (for instance, see Murray 2002a; Murray 2002b; Okubo and Levin 2001; Shigesada and Kawasaki 1997). Consequently we found three types of temporal variation of expected velocity of invaded range expansion, depending on the fractal dimension for the spatial distribution of resource patches: monotonically decreasing, monotonically decreasing, and increasing after initially decreasing.

The last case implies that we have to pay attention to the expansion of invaded region even if its velocity is observed to decrease, especially in the early period of invasion. Invader population might decrease its velocity of spatial expansion in early period and then turn to increase the velocity to expand its spatial distribution faster and faster.

It may be more realistic that a free patch would be invaded by dispersers from some *spatially neighbour* occupied patches. For instance, this may be incorporated by introducing a fractal-dimension-dependence of settlement rate. Such assumption for the location or the configuration of patches in space makes the model more difficult to be mathematically analyzed, although it must be interesting from the viewpoint of mathematical biology. This will be surely the next step of this type of mathematical model to be considered.

Some cellular automaton models or lattice models have been considered such population invasion in heterogeneous space (Bailey el al. 2000; Brown and Bolker 2004; Filipe and Gibson 1998; Filipe *et al.* 2004; Grassberger 1983; Keeling 1999; Levin and Durrett 1997; Meyers *et al.* 2003; Newman 2002; Otten *et al.* 2004; Sander *et al.* 2002; Sato *et al.* 1994; Stauffer and Aharony 1991; Tan *et al.* 2000). Computer-aided numerical analysis has been always useful in the analysis for such model, whereas numerical calculations could not necessarily derive the general result about the nature of population invasion in heterogeneous space. Only a few mathematical methods could reach some general features of such model, for instance, the mean field approximation and the pair approximation etc. (see Caraco *et al.* 2001; Filipe and Gibson 2001; Filipe *et al.* 2004; Pascual *et al.* 2002; Ovaskainen and Hanski 2001; Ovaskainen *et al.* 2002; Sato *et al.* 1994) Even though such model could be easily constructed, for instance, by a type of celluler automaton, we do not argue here such type of numeric models any more.

In this paper, we consider our mathematical model in the general context of spatial expansion of invaded range of population dispersing through spatially patchy distribution of resource. With some necessary modifications, our modeling could be easily applied for the more specified case of the spatial expansion of population distributed through a patchy/fragmentated habitats in space.

If we consider a population dynamics of sexual reproduction, we may regard the patch as the female individual or a sort of female group, which is searched by dispersing males (as for a mathematical modeling on the same standing point, for instance, see Hirata and Seno 1997). The abandonment of patch is regarded as the mated female (group) which becomes out of mating target.

For the case of prey-predator population dynamics, the patch in our model could correspond to the prey individual or group (as for the same standing point, for instance, see Russell *et al.* 1992). In this case, the prey is regarded as the resource for predator, and the abandonment of patch is as the consumption of prey by predation, or the extinction of both prey and predator in it.

In case of host-parasite population dynamics, the patch corresponds to the host individual or group under parasitism by dispersing parasites. The abandonment of patch is regarded as the parasitized host, so that this is the case when the parasitized host cannot be parasitized again without multi-parasitism.

As another contexts for the application of our model, we could consider the epidemic dynamics of disease transmission through immobile units of infection, as town, plant, etc. and classify those units into three classes: *susceptible*, *infective* and *recovered* (Koshiba and Seno 2005). Along this contexts of epidemic dynamics, the parameter β can be regarded as the infection rate from an infective unit to a susceptible one while γ can be as the recovery rate with immunity or the death rate. In this case, the invaded range considered in this paper corresponds to the range expanded by infected units, so that it means the spatial range damaged by the epidemic disease. Our modeling assumption

that the settlement rate depends only on the total number of occupied patches corresponds to, for instance, the case that the epidemic vector has a high mobility to transmit the disease, or the case that the disease transmission is through the matrix environment (e.g. wind, water or soil) surrounding susceptible units (Bailey el al. 2000; Drenth 2004; Otten *et al.* 2004). Environment-dependent way of disease transmission and the sanitary/health condition determine the nature of infected area expansion (Gilligan 2002; Keeling *et al.* 2001; van den Bosch *et al.* 1997). In case of plants or crops under attack from pests and diseases, the spatial distribution of susceptible hosts is considered as important for the spread of infection (Brown and Bolker 2004; Caraco *et al.* 2001; Drenth 2004; Jules *et al.* 2002; Otten *et al.* 2004; van den Bosch *et al.* 1997). However, little is known about the effect of environmental heterogeneity on the spatial expansion of epidemics.

For the spatial expansion of population distribution, some well-known mathematical models are of reaction-diffusion system in spatially continuous space (Murray 2002a; Murray 2002b; Okubo and Levin 2001; Shigesada and Kawasaki 1997). However, in general, it is not easy or is sometimes much tactical to introduce the nature of spatial heterogeneity of habitat distribution into such model with reaction-diffusion system. In contrast, in case of spatially discrete models, frequently constructed by cellular automaton or lattice space (Bailey el al. 2000; Brown and Bolker 2004; Filipe and Gibson 1998; Filipe *et al.* 2004; Levin and Durrett 1997; Otten *et al.* 2004; Rhodes *et al.* 1997; Sato *et al.* 1994), introduction of spatial heterogeneity is relatively easy, whereas mathematical analysis is rarely easy and becomes harder as the number of factors governing the population dynamics increases, so that a number of numerical calculations are required. Stochastic model like ours is another way for the theoretical study that could give some new insights, as some researches in landscape ecology indicate (Dunning *et al.* 1995; Fortin *et al.* 2003; Turner *et al.* 2001; Wiegand *et al.* 1999). Since there has been few models to consider the velocity of spatial expansion of invaded region over such spatially distributed patchy environment, we hope that our modeling consideration would be a pioneer approach to the problem.

APPENDIX

Applying (1), (2) and (3) with a cumbersome and careful calculation, we can derive the following partial differential equation for the probability generating function (p.g.f.) $f(x, y, t)$ defined by (21):

$$\frac{\partial f(x,y,t)}{\partial t} = \{-(\beta+\gamma)y + \gamma + \beta x y^2\}\frac{\partial f(x,y,t)}{\partial y}. \tag{A.25}$$

From (4), the initial condition is given by

$$\begin{aligned} f(x,y,0) &= \sum_{k=1}^{\infty}\sum_{h=0}^{k} P(k,h,0)x^k y^h \\ &= P(1,1,0)xy \\ &= xy. \end{aligned} \tag{A.26}$$

In addition, the following condition can be derived:

$$f(1,1,t) = \sum_{k=1}^{\infty} \sum_{h=0}^{k} P(k,h,t) = 1, \tag{A.27}$$

because the sum of probability for any possible k and h corresponds to the occurrence of any event.

With condition (A.26) and (A.27), we can solve (A.25) as follows (for instance, see p.62-63 in Bailey 1957):

$$f(x,y,t) = x \cdot \left[v_+(x) - \frac{\hat{v}(x)\{v_+(x) - y\}}{\Phi(x)} \right], \tag{A.28}$$

where

$$\begin{aligned} \Phi(x) &= \{v_+(x) - y\} + \{y - v_-(x)\} e^{-\beta x \hat{v}(x) t}; \\ \hat{v}(x) &= v_+(x) - v_-(x), \end{aligned}$$

and $v_+(x)$ and $v_-(x)$ are functions of x, given by two distinct roots of the following equation in terms of ξ:

$$\beta x \xi^2 - (\beta + \gamma)\xi + \gamma = 0.$$

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References

[1] Anderson, R.M. and May, R.M., 1986. The invasion, persistence and spread of infectious disease within animal and plant communities. *Phil. Trans. Roy. Ser. B* **314**: 533-570.

[2] Andow D.A., Kareiva, P.M., Levin, S.A. and Okubo, A., 1990. Spread of invading organisms. *Landscape Ecology* **4**: 177-188.

[3] Atkinson, C. and Reuter, G.E.H., 1976. Deterministic epidemic waves. *Math. Proc. Camb. Phil. Soc.* **80**: 315-330.

[4] Bailey, N.T.J., 1957. *The Mathematical Theory of Epidemics*, Charles Griffin & Co. Ltd., London.

[5] Bailey, D.J., Otten, W. and Gilligan, C.A., 2000. Saprotrophic invasion by the soil-borne fungal plant pathogen *Rhizoctonia solani* and percolation thresholds. *New Phytol.* **146**: 535-544.

[6] Brauer, F. and Castillo-Chávez, C., 2001. *Mathematical Models in Population Biology and Epidemiology*, Texts in Applied Mathematics 40, Springer, New York.

[7] Brown, K. and Carr, J., 1977. Deterministic epidemic waves of critical velocity. *Math. Proc. Camb. Phil. Soc.* **81**: 431-433.

[8] Brown, D.H. and Bolker, B.M., 2004. The effects of disease dispersal and host clustering on the epidemic threshold in plants. *Bull. Math. Biol.* **66**: 341-371.

[9] Caraco, T., Duryea, M.C and Glavanakov, S., 2001. Host spatial heterogeneity and the spread of vector-borne infection. *Theor. Pop. Biol.* **59**: 185-206.

[10] Diekmann, O. and Heesterbeek, J.A.P., 2000. *Mathematical Epidemiology of Infectious Diseases: Model Building, Analysis and Interpretation*, Wiley Series in Mathematical and Computational Biology, John Wiley & Son, Chichester.

[11] Drenth, A., 2004. Fungal epidemics — does spatial structure matter? *New Phytol.* **163**: 4-7.

[12] Dunning, J.B., Stewart, D.J., Danielson, B.J., Noon, B.R., Root, T.L., Lamberson, R.H. and Stevens, E.E., 1995. Spatially explicit population models: Current forms and future uses. *Ecological Applications* **5**: 3-11.

[13] Dwyer, G., Elkinton, J.S. and Buonaccorsi, J.P., 1997. Host heterogeniety in susceptibility and disease dynamics: tests of a mathematical model. *Am. Nat.* **150**: 685-707.

[14] Fagan, W.F., Lewis, M.A., Neubert, M.G. and van den Driessche, P., 2002. Invasion theory and biological control. *Ecology Letters* **5**: 148-157.

[15] Filipe, J.A.N. and Gibson, G.J., 1998. Studying and approximating spatio-temporal models for epidemic spread and control. *Phil. Trans. R. Soc. Lond. B* **353**: 2153-2162.

[16] Filipe, J.A.N. and Gibson, G.J., 2001. Comparing approximations to spatio-temporal models for epidemics with local spread. *Bull. Math. Biol.* **63**: 603-624.

[17] Filipe, J.A.N., Gibson, G.J. and Gilligan, C.A., 2004. Inferring the dynamics of a spatial epidemic from time-series data. *Bull. Math. Biol.* **66**: 373-391.

[18] Fortin, M.-J., Boots, B., Csillag, F. and Remmel, T.K., 2003. On the role of spatial stochastic models in understanding landscape indices in ecology. *Oikos* **102**: 203-212.

[19] Gautestad, A.O. and Mysterud, I., 1994. Fractal analysis of population ranges: methodological problems and challenges. *Oikos* **69**: 154-157.

[20] Gilligan, C.A., 2002. An epidemiological framework for disease management. *Adv. Bot. Res.* **38**: 1-64.

[21] Grassberger, P., 1983. On the critical-behaviour of the general epidemic process and dynamical percolation. *Math. Biosci.* **63**: 157-172.

[22] Hanski, I., 1994. Patch occupancy dynamics in fragmented landscapes. *Trends Ecol. Evol.* **9**: 131-135.

[23] Hanski, I., 1994. A practical model for metapopulation dynamics. *J. Anim. Ecol.* **63**: 151-162.

[24] Hanski, I., 1999. *Metapopulation Ecology*, Oxford University Press, Oxford.

[25] Haskell, J.P., Ritchle, M.E. and Olff, H., 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature* **418**: 527-530.

[26] Hastings, H.M. and Sugihara, G., 1993. *Fractals: A User's Guide for the Natural Sciences*, Oxford University Press, New York.

[27] Hirata, H. and Seno, H., 1997. How does the size distribution of male territories depend on the spatial distribution of females? *Ecol. Modelling* **103**: 193-207.

[28] Jeger, M.J., 1989. *Spatial Component of Plant Disease Epidemics*, Prentice-Hall, Englewood Cliffs.

[29] Johnson, A.R., Wiens, J.A., Milne, B.T. and Crist, T.O., 1992. Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology* **7**: 63-75.

[30] Jules, E.S., Kauffman, M.J., Ritts, W.D. and Carroll, A.L., 2002. Spread of an invasive pathogen over a variable landscape: A nonnative root rot on Port Orford cedar. *Ecology* **83**: 3167-3181.

[31] Keeling, M.J., 1999. The effects of local spatial structure on epidemiological invasions. *Proc. R. Soc. Lond. B* **266**: 859-867.

[32] Keeling, M.J., Woolhouse, M.E.J., Shaw, D.J., Matthews, L., Chase-Topping, M., Haydon, D.T., Cornell, S.J., Kappey, J., Wilesmith, J. and Grenfell, B.T., 2001. Dynamics of the 2001 UK foot and mouth epidemic: Stochastic dispersal in a heterogeneous landscape. *Science* **294**: 813-817.

[33] Keymer, J.E., Marquet, P.A., Velasco-Hernández, J.X. and Levin, S.A., 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. *Am. Nat.* **156**: 478-494.

[34] Koshiba, S. and Seno, H., 2005. *A mathematical model for spatially expanding infected area of epidemics transmitted through heterogeneously distributed susceptible units. J. Biol. Syst.* (in press)

[35] Kot, M. and Schaffer, W.M., 1986. Discrete-time growth-dispersal models. *Math. Biosci.* **80**: 109?136.

[36] Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* **73**: 1943-1967.

[37] Levin, S.A. and Durrett, R., 1997. From individuals to epidemics. *Phil. Trans. R. Soc. Lond. B* **351**: 1615-1621.

[38] Mandelbrot, B.B., 1982. *Fractal Geometry of Nature*, W.H. Freeman and Company, New York.

[39] Medlock, J. and Kot, M., 2003. Spreading disease: integro-differential equations old and new. *Math. Biosci.* **184**: 201?222.

[40] Metz, J.A.J., Mollison, D. and van den Bosch, F., 1999. The dynamics of invasion waves. *INTERIM REPORT* **IR-99-039**.

[41] Meyers, L.A., Newman, M.E.J., Martin, M. and Schrag, S., 2003. Applying network theory to epidemics: Control measures for *Mycoplasma pneumoniae* outbreak. *Emerging Infectious Diseases* **9**: 204-210.

[42] Mollison, D., 1977. Spatial contact models for ecological and epidemic spread. *J. R. Statist. Soc. B* **39**: 283-326.

[43] Morse, D.R., Lawton, J.H., Dodson, M.M. and Williamson, M.H., 1985. Fractal dimension of vegetation and the distibution of arthropod body lengths. *Nature* **314**: 731-733.

[44] Murray, J.D., 2002. *Introduction to Mathematical Biology*, Interdisciplinary Applied Mathematics 17, Springer, New York.

[45] Murray, J.D., 2002. *Mathematical Biology: Spatial Models and Biomedical Applications, 3rd Edition*, Interdisciplinary Applied Mathematics 18, Springer, New York.

[46] Neubert, M.G., Kot, M. and Lewis, M.A., 2000. Invasion speeds in fluctuating environments. *Proc. R. Soc. Lond. B* **267**: 1603-1610.

[47] Neuhauser, C., 2001. Mathematical challenges in spatial ecology. *Notices of The AMS* **48**: 1304-1314.

[48] Newman, M.E.J., 2002. Spread of epidemic disease on networks. *Phys. Rev. E* **66**: 016128.

[49] Okubo, A. and Levin, S.A., 2001. *Diffusion and Ecological Problems: Modern Perspectives, Second Edition*, Interdisciplinary Applied Mathematics 14, Springer, New York.

[50] O'Neill, R.V., Milne, B.T., Turner, M.G. and Gardner, R.H., 1988. Resource utilization scales and landscape pattern. *Landscape Ecology* **2**: 63-69.

[51] Otten, W., Bailey, D.J. and Gilligan, C.A., 2004. Empirical evidence of spatial thresholds to control invasion of fungal parasites and saprotrophs. *New Phytol.* **163**: 125-132.

[52] Ovaskainen, O. and Hanski, I., 2001. Spatially structured metapopulation models: global and local assessment of metapopulation capacity. *Theor. Pop. Biol.* **60**: 281-304.

[53] Ovaskainen, O., Sato, K., Bascompte, J. and Hanski, I., 2002. Metapopulation models for extinction threshold in spatially correlated landscapes. *J. theor. Biol.* **215**: 95-108.

[54] Palmer, M.W., 1988. Fractal geometry: a tool for describing spatial patterns of plant communities. *Vegetatio* **75**: 91-102.

[55] Pascual, M., Roy, M. and Franc, A., 2002. Simple temporal models for ecological systems with complex spatial patterns. *Ecology Letters* **5**: 412-419.

[56] Rhodes, C.J., Jensen, H.J. and Anderson, R.M., 1997. On the critical behaviour of simple epidemics. *Proc. R. Soc. Lond. B* **264**: 1639-1646.

[57] Russell, R.W., Hunt, Jr., G.L., Coyle, K.O. and Cooney, R.T., 1992. Foraging in a fractal environment: Spatial patterns in a marine predator-prey system. *Landscape Ecology* **7**: 195-209.

[58] Sander, L.M., Warren, C.P., Sokolov, I.M., Simon, C. and Koopman, J., 2002. Percolation on heterogeneous networks as a model for epidemics. *Math. Biosci.* **180**: 293-305.

[59] Sato, K., Matsuda, H. and Sasaki, A., 1994. Pathogen invasion and host extinction in lattice structures populations. *J. Math. Biol.* **32**: 251-268.

[60] Seno, H., 1993. Stochastic model for colony dispersal. *Anthropol. Sci.* **101**: 65-78.

[61] Seno, H. and Matsumoto, H., 1996. Stationary rank-size relation for community of logistically growing groups. *J. Biol. Systems* **4**: 83-108.

[62] Shigesada, N. and Kawasaki, K., 1997. *Biological Invasions: Theory and Practice*, Oxford University Press, New York.

[63] Stauffer, D. and Aharony, A., 1991. *Introduction to Percolation Theory*, Taylor & Francis, London.

[64] Sugihara, G. and May, R.M., 1990. Application of fractals in ecology. *Trends Ecol. Evol.* **5**: 79-86.

[65] Tan, Z.-J., Zou, X.-W. and Jin, Z.-Z., 2000. Percolation with long-range correlations for epidemic spreading. *Phys. Rev. E* **62**: 8409-8412.

[66] Turner, M.G., Gardner, R.H. and O'Neill, R.V., 2001. *Landscape Ecology in Theory and Practice: Pattern and Process*, Springer-Verlag, New York.

[67] van den Bosch, F., Mets, J.A.J. and Zadoks, J.C., 1997. Pandemics of focal plant disease: A model. *INTERIM REPORT* **IR-97-083**.

[68] Wiegand, T., Moloney, K.A., Naves, J. and Knauer, F., 1999. Finding the missing link between landscape structure and population dynamics: A spatially explicit perspective. *Am. Nat.* **154**: 605-627.

[69] With, K.A., 1994. Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecology* **9**: 25-36.

[70] With, K.A. and King, A.W., 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* **13**: 314-326.

[71] With, K.A., 2002. The landscape ecology of invasive spread. *Conservation Biology* **16**: 1192-1203.